THE RELATIONSHIPS OF THE QUOKKA *(SETONIX BRACHYURUS)*

By G. B. SHARMAN, Department of Zoology, University of Western Australia.

INTRODUCTION

The macropod marsupial genus *Setonix* is represented by the single species *Setonix brachyurus* (Quoy and Gaimard) — the Quokka of South-western Australia. The relationships of *Setonix* are rather obscure and authorities have not reached general agreement as to its phylogenetic position. It is not, however, intended, in this paper, to assess the relative merits of the conclusions drawn by earlier workers but rather to put forward some new evidence based on characters not hitherto considered. Museum collections of mammals are often limited to skins and skeletal material, the internal organs being discarded. Consequently phylogenetic studies are usually based only on dentition, foot structure or other external characters. These are, however, subject to some limitations. Thus the Bandicoots (Peramelidae) show a polyprotodont dental condition allying them to the carnivorous Native Cats and Wambengers (Dasyuridae), but have the same syndactylous foot arrangement as the herbivorous maruspials. The dentition of *Setonix* closely resembles that of the Tree Kangaroos *(Dendrolagus)* but the similarities may merely reflect similar feeding habits in taxonomically widely separated genera.

It has been shown in many groups of organisms, that the chromosome number is a relatively stable character which provides a reliable guide to the relationships of the various species. A list of known chromosome numbers in marsupials has been published (Sharman and Barber, 1953) and reference to this (with some additional unpublished data) indicates the chromosome number to be a relatively stable character. Thus assemblages of marsupials characterised by the same chromosome number include the American Didelphidae (with a diploid number of 22 chromosomes), the Dasyuridae (14 chromosomes) and the Peramelidae which also have 14 chromosomes but which differ from the Dasyuridae in the morphology of the sex chromosomes. Within the Australian Possums (Phalangeridae) and Kangaroos (Macropodidae) various chromosome numbers are found but certain groups of species are characterised by a constant number. Some members of these latter families have 22 chromosomes, like the Didelphidae, but this American group differs from all Australian species so far studied in having all rod-shaped chromosomes (i.e. with subterminal centromeres).

The danger of attaching great phyletic importance to tooth and foot structure which are readily susceptible to modifications associated with habitat, has been stressed by various authorities (e.g. Gregory, 1910). Gregory considers the urogenital system, brain and skull present more reliable evidence of phyletic relationships. Pearson (1945 and later papers) has emphasised the stability of the urogenital system and its importance as a guide to the relationships within the marsupials. In this paper I have attempted to assess the relationships of *Setonix* by a comparison of its chromosome number and urogenital system with those of related species.

Bensley (1903) showed that *Setonix* resembled *Dendrolagus* in the characters of the incisors, molars and sectorial premolars. He considered, however, that the small size, complete absence of canine teeth, terrestrial character of the pes, and distribution of *Setonix* removed it from close relationship to *Dendrolagus*. He concluded *Setonix* to be a member of "the Small Wallaby section of genus *Macropus* which has assumed feeding habits similar to those of the tree-living *Dendrolagus*." Bensley followed Thomas (1888) in dividing the genus *Macropus* into small wallabies, large wallabies and kangaroos. Although the Kangaroos *(Macropus)* and Wallabies (now usually elevated to generic level as *Protemnodon (=Wallabia)* are homogeneous groups the small wallaby section is not. Thomas included here *eugenii* (the Tammar of S.W. Australia) and the allied species *parma* now shown, in spite of their small size, to belong to *Protemnodon* (Raven and Gregory, 1946; Tate, 1948).

Wood Jones (1924) followed Bensley in dividing the larger macropod marsupials into brachyodont and hypsodont series. This author does not, however, acknowledge the possibility of convergence in the teeth patterns and places *Setonix* together with *Dendrolagus* and *Dorcopsis* in his classification. Raven and Gregory (1946) note the convergent resemblances between *Setonix* and the Rat Kangaroos but state that its nearest relatives belong to *Thylogale,* which genus they include in the brachyodont section with the Quokka and the Tree Kangaroos. Tate (1948), however, does not agree with any of the above authors and regards *Setonix* as a derivative of *Protemnodon,* probably of the *P. eugenii* group. This author, discussing Wood Jones' placing of *Setonix* in the brachyodont section as opposed to the hypsodont section, states that he is unable to appreciate this distinction in practice.

Systematic works on the macropod marsupials are numerous and no complete agreement has yet been reached with regard to the delimitation of genera. There appears to be no justification for the extreme splitting of Iredale and Troughton (1934) who have divided the genus *Macropus,* as Bensley (1903) understood it, into no less than five genera. In this paper I have followed the classification of Simpson (1945).

THE DISTRIBUTION OF *SETONIX BRACHYURUS*

Setonix brachyurus was once widely distributed in the South-west of Western Australia (Shortridge, 1909). Today it appears to be common only on Rottnest and Bald Islands although isolated colonies exist in some mainland areas. Early in 1954 a skull of *Setonix* was brought from Toolbrunup in the Stirling Ranges by a member of this department. Other naturalists *(W.A. Nat.,* vol. 4, 1954, pp. 128-141) have reported seeing specimens and the positive identification of these animals would be of interest with regard to establishing the present distribution of *Setonix*. White (1952) has discussed the status and past abundance of the Quokka in S.W. Australia.

When Bald and Rottnest Island animals are seen side by side in captivity certain differences are apparent. The Bald Island animals appear to have a thinner and shorter tail and a slightly different shaped head when compared to Rottnest animals. Measurements of head and body and tail length, however, fail to show any constant differences in body proportions. No colour differences are apparent but the fur of the Bald Island animals appears to be softer than in animals from Rottnest.

When the skulls of fully grown Bald and Rottnest Island animals are compared there are, in the small sample available for study, some differences which appear constant (Fig. 1, Table 1). In six Bald Island skulls (1 ♂, 5 unknown sex) examined the maxilla is between 2.7 and 3.1 times the length of the premaxilla with a mean of 2.9. In twelve Rottnest skulls (2 ♂, 10 ♀) the proportions of length of premaxilla to length of maxilla vary from 2.0 to 2.6 (mean 2.2). Through the courtesy of Mr. L. Glauert, Curator of the W.A. Museum, I have examined skulls of 5 mainland specimens (2 ♂, 2 ♀, 1 unknown sex). One other mainland specimen of unknown sex has also been examined. These specimens have been collected at various mainland localities and the proportions of the lengths of maxillary bones vary between 1 : 2.2 and 1 : 2.7 (mean 1 : 2.4). From these figures it could, perhaps, be concluded that the mainland population is intermediate between

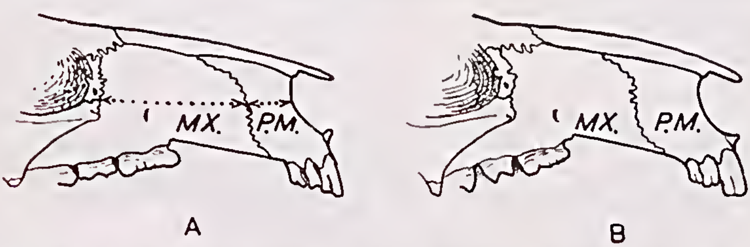

Fig. 1.—A comparison of the anterior skull region in an animal from Bald Island (A) and an animal from Rottnest (B). Note the short premaxilla (P.M.) in the Bald Island skull compared to the same bone in the Rottnest skull. The lengths of maxilla (MX.) and premaxilla were measured along the dotted lines shown in A. Both figures x 1.

TABLE 1—LENGTHS OF MAXILLA AND PREMAXILLA IN SETONIX

Locality	No. of skulls measured	Mean length of maxilla	Mean length of premaxilla	Length maxilla / Length premaxilla
Bald Island	6	18.5 mm.	6.3 mm.	2.9
Mainland, S.W. Aus.	6	17.2 ,,	7.2 ,,	2.4
Rottnest Island	12	16.1 ,,	7.3 ,,	2.2

the two island populations, with regard to this character, but the sample is small and by no means representative considering the previous wide distribution of *Setonix*. Alternatively, when a large series is measured, it may be found that the whole population of *Setonix* can be considered as a cline with the Rottnest and Bald Island animals near the extremes. It is proposed to examine further material and prepare a full taxonomic analysis later.

THE CHROMOSOME NUMBER

Drummond (1933) showed the Quokka to have 22 chromosomes and this has been confirmed on material from both Bald and Rottnest Islands (Fig. 2A). The sex chromosomes (X and Y) are among the smallest of the set and the majority of the autosomes have near terminal centromeres. The Tasmanian Pademelon (*Thylogale billardierii*) also has 22 chromosomes (McIntosh and Sharman, 1953) and these appear morphologically similar to the chromosomes of *Setonix*.

Fig. 2—The chromosomes of *Setonix brachyurus*, 2 N = 22 (A) and *Protemnodon eugenii*, 2 N = 16 (B). X and Y denote the sex chromosomes. Both figures drawn from male spermatogonial mitoses (x 2,250).

The chromosome number in the Tammar (*Protemnodon eugenii*) is 16 (Fig. 2B). The Sandy Wallaby (*P. agilis*) and the Brush (*P. irma*) also have 16 chromosomes as have *P. elegans* (Matthey, 1934) and the Red-necked Wallaby (*P. rufogrisea*) (McIntosh and Sharman, 1953). The findings of Raven and Gregory (1946) and Tate (1948) who removed *eugenii* from *Thylogale* to *Protemnodon* are thus confirmed on cytological grounds. Troughton (1954) follows Iredale and Troughton (1934) in placing *eugenii* in the genus *Thylogale*. For this there can be no justification unless the size of the animal is regarded as being of prime importance in determining its relationships.

The derivation of *Setonix* from the *P. eugenii* group as suggested by Tate (1948) does not appear likely when the chromosome numbers are considered. Cytological evidence makes it far more likely that Raven and Gregory (1946) correctly stated the relationships of *Setonix* when they emphasised its resemblances to *Thylogale*. Of the Macropodinae studied cytologically only *T. billardierii* and *Setonix* have 22 chromosomes, nine other species have less than 22. Two of the four Phalangeridae whose cytology is known have 22 chromosomes and this, perhaps, indicates that *Thylogale* and *Setonix* are closer to the Phalangers than are the remaining present-day Macropodinae.

THE FEMALE UROGENITAL SYSTEM

The anatomy of the urogenital system in the female marsupial differs fundamentally from the plan found in the higher (eutherian) mammals. In the marsupials the ureters pass between the embryonic Mullerian ducts (Fig. 3A) which later in life become specialised as oviducts, uteri and vaginae. In the eutherian mammals the ureters pass outside the Mullerian ducts which become fused in the vaginal region to form a single structure. The fusion of the lateral vaginae of marsupials into a common structure is impossible owing to the position of the ureters, but in spite of this primary obstacle a median vaginal structure has been developed. This has been achieved by the elongation and development of the anterior vaginal culs-de-sac (Fig. 3A). At birth the embryo passes from the culs-de-sac through the intervening tissue directly to the urogenital sinus, the passage thus opened, lying between the ureters, being called the pseudo-vaginal canal. The distance separating the lower end of the culs-de-sac from the urogenital sinus (the pseudo-vaginal gap) is variable, being greater in the more primitive marsupials. In *Setonix*, and probably in all other macropod marsupials, the pseudo-vaginal canal remains permanently open after the first parturition.

The urogenital system of *Setonix* has previously been described (Waring *et al.*, 1955). The following description only deals with those parts of the vaginal complex which are compared with like structures in the Common Possum *(Trichosurus vulpecula)* and the Tammar *(Protemnodon eugenii)*. The vaginal structures of the three species are shown in diagram form in Fig 3. The diagrams represent the oestrous condition as found in parous females.

Anterior vaginal canals. In *Protemnodon eugenii* and in other kangaroo-like marsupials (Pearson 1950), the anterior vaginal canals become enormously hypertrophied at oestrus and serve as ducts for the reception of spermatozoa. In the oestrous specimen described here (Fig. 3C) the anterior vaginal canals are of several hundred times greater diameter than at other phases of the oestrous cycle and are entirely filled with seminal fluid. In the oestrous *Trichosurus* (Fig. 3B) the anterior vaginal canals, though large are not as hypertrophied as in *Protemnodon*. In the oestrous *Setonix* (Fig. 3D) they remain of small diameter.

Vaginal culs-de-sac. In all three species the culs-de-sac are distended and contain abundant seminal fluid. Those of *Trichosurus* are larger than in either of the above species and from them a large swollen diverticulum full of spermatozoa projects in a ventral direction so that a longitudinal section (Fig. 3B) inadequately illustrates the actual condition. *Setonix* and *Protemnodon* show similar degrees of enlargement of the culs-de-sac. Two of the three specimens of *Trichosurus* examined were parous but an

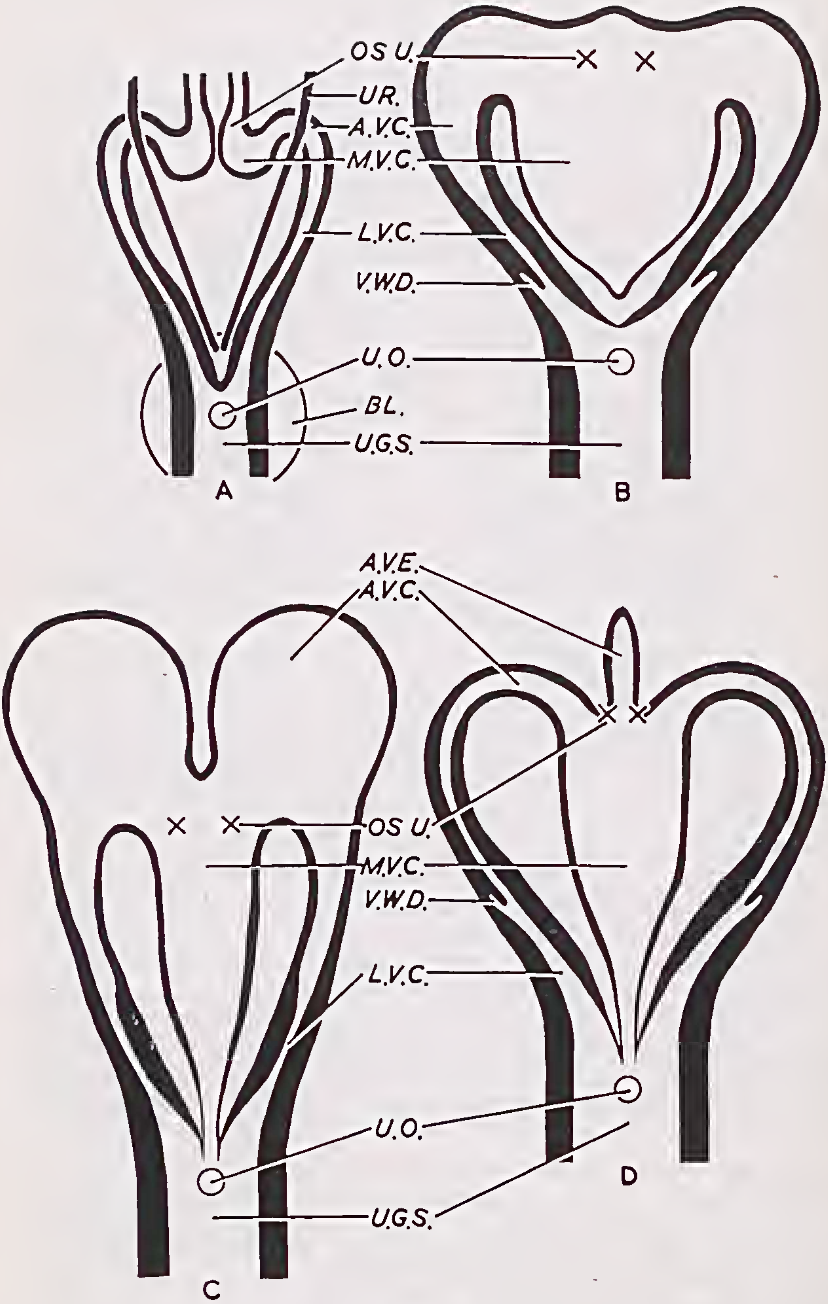
OS U.
UR.
A.V.C.
M.V.C.
L.V.C.
V.W.D.
U.O.
BL.
U.G.S.
A
B
A.V.E.
A.V.C.
OS U.
M.V.C.
V.W.D.
L.V.C.
U.O.
U.G.S.
C
D

FIG. 3.

examination of these revealed a closed median vaginal canal (Fig. 3B). *Trichosurus* thus differs from another phalanger, the Honey Mouse *(Tarsipes),* in which the pseudo-vaginal canal remains open after parturition (de Bavay, 1951).

Lateral vaginal canals. In all three species these have thick muscular walls. Those of *Setonix* and *Trichosurus* share one common feature not found in *P. eugenii* in that a short blind diverticulum (Fig. 3, V.W.D.) is present. This is probably the caudal remnant of the Wolffian duct which occurs as a constant feature in the lateral vaginae of many dasyurids (Pearson and de Bavay, 1953). de Bavay (1951) has described the reproductive system of an adult *Tarsipes* in which the embryonic Wolffian duct has been retained. de Bavay considers the specimen to have been abnormal, and this appears likely since other specimens do not show a similar condition. No trace can be found of this remnant in *Protemnodon* nor have I been able to confirm its presence in the vaginal complex of any adult macropod other than *Setonix,* where it is always present.

Anterior vaginal expansion. Setonix appears unique amongst the Macropodinae in possessing an anterior vaginal expansion. It is not known whether this structure is homologous with the structures of the same name described by Pearson (1945) in the Rat Kangaroos (Waring *et al.,* 1955). Spermatozoa are found in the anterior vaginal expansion following copulation.

LEGEND TO FIG. 3

A.—Hypothetical primitive vaginal condition in marsupials, dorsal view. Anterior vaginal canals not fused and showing little development of the culs-de-sac. The ureters pass over the anterior vaginal canals and between the lateral vaginal canals before joining the bladder, which lies in a ventral position.

B.—Vaginal complex of *Trichosurus vulpecula* drawn from a parous specimen in oestrus. Note the large median vaginal culs-de-sac and vestigial Wolffian duct. Sagittal section (x 2½).

C.—Vaginal complex of *Protemnodon eugenii* drawn from a parous specimen in oestrus and showing the greatly hypertrophied anterior vaginal canals. Sagittal section (x 1).

D.—Vaginal complex of *Setonix brachyurus* drawn from a parous specimen in oestrus. Note the enlarged median vaginal culs-de-sac, vestigial Wolffian duct and resemblance to the vaginal complex of *Trichosurus vulpecula.* Sagittal section (x 2½).

A.V.C. .... anterior vaginal canal.
A.V.E. .... anterior vaginal expansion.
BL. .... bladder.
L.V.C. .... lateral vaginal canal.
M.V.C. .... median vaginal culs-de-sac.
OS.U. .... position of os uterus.
U.O. .... position of opening of bladder into urogenital sinus.
U.G.S. .... urogenital sinus.
UR. .... ureter.
V.W.D. .... vestigial Wolffian duct.

DISCUSSION

Previous authorities have not found agreement as to the phyletic position of the genus *Setonix*. This study supports the conclusions of Raven and Gregory who believe the closest relatives of *Setonix* are to be found in the genus *Thylogale*. The affinities, as shown by the chromosome number, definitely support this hypothesis. I believe, however, that even more interesting evidence of relationships is shown by the morphology of the vaginal complex. A relatively primitive state is seen in *Setonix* where the anterior vaginal canals do not show the specialised condition found in *Protemnodon* and many other macropods. I have not had available for study a reproductive system from an oestrous *Thylogale,* but through the courtesy of Dr. J. Pearson, then director of the Tasmanian Museum, I have carried out a brief examination of one of his specimens of the Tasmanian Pademelon *(T. billardierii),* taken shortly after copulation. The anterior vaginal canals show the same specialised condition as is found in the Tammar *(Protemnodon eugenii).* Pearson (1946) has described the reproductive system of *Thylogale billardierii* but does not record the presence of vestigial Wolffian ducts in this species. A re-examination to find whether these are present would be of interest. It is however sufficient, for the purpose of this paper, to record the similarities between the vaginal complex of *Setonix* and the phalanger *Trichosurus vulpecula.* Adults of both have a vestigial Wolffian duct and in both the main region used for the reception of spermatozoa, by the oestrous female, is the median vaginal culs-de-sac. It is generally conceded that the Macropodidae rose from phalanger-like ancestors and the presence of these phalangerine characters in the reproductive system of *Setonix* indicate that, in spite of some specialised characters (e.g. dentition), this genus must be regarded as rather close to the stem from which the remaining kangaroo-like marsupials arose. It is here unnecessary to discuss the question as to which of the macropod groups — Macropodinae and Potoroinae (Rat Kangaroos) are the more primitive. Probably they are in a sense parallel groups sharing a phalanger-like ancestor. Pearson (1946, 1950) in studies of four of the five living genera of Rat Kangaroos has drawn attention to the specialised characters of their urogenital systems which appear to preclude this group as direct ancestors of the Macropodinae.

It is concluded from this study that the nearest relatives of *Setonix* are probably to be found in the genus *Thylogale.* The unspecialised nature of the reproductive system of *Setonix* and the common features shared with the phalangers, however, indicate a more primitive phylogenetic position than that of *Thylogale.* Thus *Setonix* may be considered to share common features with the stock from which *Thylogale* and hence the Kangaroos *(Macropus)* and Wallabies *(Protemnodon)* arose. The relationship of *Setonix* and *Thylogale* postulated here is not untenable on zoogeographic grounds. Most S.W. Australian animals have their counterparts in the fauna of Eastern Australia. An analysis of this type of distribution has been made for species-pairs of birds (Serventy, 1953). The Quokka antedates this distribution and represents a more ancient fauna, the eastern counterpart of which does not exist. The Western Australian King Parrot *(Purpureicephalus)* (Serventy and Whittell, 1951, p. 59) may be taken as a representative of this same distribution. Other elements in S.W. Australia agree with this interpretation and may be taken as representing the truly autochthonian fauna (A. R. Main, ms.).

This study was made while the author held a research fellowship financed by a grant from the Nuffield Foundation to whom grateful acknowledgment is made.

LITERATURE CITED

de Bavay, J. M., 1951. Notes on the female urogenital system of *Tarsipes spenserae* (Marsupialia). *Pap. Roy. Soc. Tasm. 1950,* pp. 143-150.

Bensley, B. A., 1903. On the evolution of the Australian Marsupialia; with remarks on the relationships of marsupials in general. *Trans Linn. Soc. Lond. (Zool.) 9,* pp. 83-217.

Drummond, F. H., 1933. The male meiotic phase in five species of marsupials. *Quart. J. Micr. Sci. 76,* pp. 1-11.

Gregory, W. K., 1910. The orders of mammals. *Bull. Am. Mus. Nat. Hist. 91,* pp. 1-524.

Iredale, T., and Troughton, E. Le G., 1934. A check list of mammals recorded from Australia. *Aust. Mus. Sydney, Mem. VI.*

McIntosh, A. J., and Sharman, G. B., 1953. The chromosomes of some species of marsupials. *J. Morph. 93,* pp. 509-531.

Matthey, R., 1934. La formula chromosomiale du kangourou *Macropus parryi* Benn. *C.R.S. Biol. 117,* pp. 406-407.

Pearson, J., 1945. The female urogenital system of the Marsupialia with special reference to the vaginal complex. *Pap. Roy. Soc. Tasm. 1944,* pp. 71-98.

Pearson, J., 1946. The affinities of the rat-kangaroos (Marsupialia) as revealed by a comparative study of the female urogenital system. *Pap. Roy. Soc. Tasm. 1945,* pp. 13-25.

Pearson, J., 1950. The relationships of the Potoroidae to the Macropodidae (Marsupialia). *Pap. Roy. Soc. Tasm. 1949,* pp. 211-229.

Pearson, J., and de Bavay, J. M., 1953. The urogenital system of the Dasyurinae and Thylacininae. *Pap. Roy. Soc. Tasm. 87,* pp. 175-199.

Raven, H. C., and Gregory. W. K., 1946. Adaptive branching of the kangaroo family in relation to habitat. *Amer. Mus. Novitates,* no. *1309,* pp. 1-33.

Sharman, G. B., and Barber, H. N., 1953. Multiple sex chromosomes in the marsupial, *Potorous. Heredity, 6,* pp. 345-355.

Serventy, D.L., 1953. Some Speciation Problems in Australian Birds. *Emu,* 53, pp. 131-145.

Serventy, D. L., and Whittell, H. M., 1951. *A Handbook of the Birds of Western Australia,* 2nd edn. (Paterson, Perth).

Shortridge, G. C., 1909. An account of the geographical distribution of the marsupials and monotremes of South-West Australia, having special reference to the specimens collected during the Balston expedition of 1904-1907. *Proc. Zool. Soc. Lond. 1909,* pp. 803-848.

Simpson, G. G., 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist. 85,* pp. 1-350.

Tate, G. H. H., 1948. Studies on the anatomy and phylogeny of the Macropodidae (Marsupialia). *Bull. Am. Mus. Nat. Hist. 91*, pp. 239-351.

Thomas, O., 1888. Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History). *London, British Museum (Natural History)*, 1-401.

Troughton, E., 1954. *Furred Animals of Australia*, 5th (revised) Edition. (Angus and Robertson: Sydney).

Waring, H., Sharman, G. B., Lovat, D., and Kahan, M., 1955. Studies on marsupial reproduction. 1. General features and techniques. *Aust. J. Zool. 3* (in the press).

White, S. R., 1952. The Occurrence of the Quokka in the South-west. *W.A. Nat. 3*, pp. 101-103.

Wood Jones, F., 1924. *The Mammals of South Australia. Pt. 2.* (Govt. Printer: Adelaide).

APPENDIX

MEASUREMENTS OF THE MAXILLARY IN A SERIES OF SKULLS OF SETONIX BRACHYURUS

Locality	No.	Sex	Length of maxilla (mm.)	Length of pre-maxilla (mm.)	Ratio of Max. to P.M.
Rottnest Is	1	♂	16.0	8.0	2.0
,,	2	♂	16.5	7.5	2.2
,,	3	♀	16.0	7.0	2.3
,,	4	♀	16.0	7.5	2.1
,,	5	♀	15.5	7.5	2.1
,,	6	♀	17.0	6.5	2.6
,,	7	♀	16.0	7.0	2.3
,,	8	♀	15.0	7.5	2.0
,,	9	♀	17.5	7.5	2.3
,,	10	♀	16.0	7.5	2.1
,,	11	♀	14.5	7.0	2.1
,,	12	♀	17.0	7.0	2.4
Mean. Rottnest Is.			16.1	7.3	2.2
Mundaring Weir	M1285	♀	17.0	7.5	2.2
Capel	M1063	♂	16.5	7.5	2.2
Karridale	M1121	♀	17.0	6.5	2.6
Toolbrunup	Msm1	?	17.0	7.0	2.4
Big Grove, King George's Sound	M518	♂	15.5	7.0	2.2
?	M1869	?	20.0	7.5	2.7
Mean. Mainland			17.2	7.2	2.4
Bald Is.	1	♂	18.5	6.0	3.1
,,	2	?	17.5	6.0	2.9
,,	3	?	19.0	6.5	2.9
,,	4	?	17.5	6.5	2.7
,,	5	?	20.0	7.0	2.9
,,	6	?	18.5	6.0	3.1
Mean. Bald Is.			18.5	6.3	2.9